CAPILLARY PATTERNS IN VERTEBRATES

Andrew W. Ansara

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Thesis

CAPILLARY PATTERNS IN VERTEBRATES

by

Andrew William Ansara
(A. B. Boston University, 1946)

submitted in partial fulfilment of the
requirements for the degree of
Master of Arts
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INTRODUCTION

The study of capillaries had been neglected for many years. Only within comparatively recent times, approximately thirty years, has interest in capillaries been "rediscovered". Work in this field, according to Krogh (1924), was taken up by researchers almost simultaneously in different countries.

The study of blood vessels is traced back to Harvey's discovery (1624) of the circulation of the blood. Nothing was known, however, of the presence of capillaries until nine years later, when Malpighi (1635) discovered them. Very little more of importance was done in the way of studies of the minute blood vessels until a much later date. One of the earliest accounts was presented in 1805 when Moreau published the works and studies of Vicq D'Azyr who did a considerable

amount of investigation relating to capillary morphology. The first important contribution to capillary study occurred in 1873 when Rouget described the perivascular cells surrounding the capillary wall. In 1883, Stricker performed several outstanding experiments on capillary function.

The "rediscovery" of capillaries commenced around 1919, when Krogh did research on the number and distribution of capillaries in muscles. In 1921, Hooker did work on the function of capillaries. Krogh's classic "Anatomy and Physiology of Capillaries" (1924) paved the way for future workers, and today, research in this field is carried on extensively.

It has proved to be a most fruitful field, for many new theories concerning capillaries, both morphological and physiological, have been evolved. It is only natural, therefore, that some attempt be made to correlate these theories, sift and weigh evidence and interpret the results.

Among the theories concerning capillaries is the belief that they are specialized for separate functions in diverse regions in the body. Hooker (1921), as mentioned above, gave an extensive account regarding the diversity of function of capillaries. This theory has been gaining greater support, and much work is being done and is still to be done before any definite conception can be established.

This paper shall deal with one aspect of capillaries, namely, their patterns in selected regions within the body.

CAPILLARIES--A GENERAL SURVEY

In this paper, the term capillaries and capillary vessels will be used to include all purely endothelial tubing normally lying between the arterioles and venules. The walls of these vessels are composed of a single layer of endothelial cells (Fig. 1). These cells, according to Chambers and Zweifach (1946), posess a cellular tone which gives a certain degree of elasticity to the walls of the capillaries.

Capillary endothelial cells differ in shape, depending upon their location and function. For example, in wide capillaries, the individual cells are short and broad. In capillaries of medium width, two cells may surround the aperture. In narrow capillary vessels, only one cell may be found surrounding the entire wall.

The origin of the first capillaries is from the embryonic connective tissue. (Sabin 1920). Perithelium, a connective tissue of collagenous or reticular fibers, surrounds the developing vessels, protecting them from the secretions of neighboring tissues.

After a certain period of time, there may be a certain amount of degeneration in a number of capillary vessels. The capillaries become less permeable (Holman, 1937). Advancing growth of the vessels is generally marked by hemorrhages. (Sandison, 1928-a). Re-growth probably takes place by the sending out of sprouts from pre-existing capillaries, following

the procedure occuring in the tails of tadpoles, (Sandison, 1928-b).

Rouget cells, called such after their discoverer by Vimtrup (1922), and which are a specialized type of pericapillary cells probably containing reticulo-endothelial elements, may sometimes be observed. These have long branching processes which surround the capillary wall. (Fig. 2). It was once believed (Rouget. 1873), that these were contractile elements, being directly responsible for a change in tonus in capillaries. Thus, it was thought for many years that capillaries have independent contractility (Stricker, 1883, Krogh, 1924, Landis, 1934 and others). These workers believe that the Rouget cells give capillaries their independent tonus. Other workers holding this same opinion are Schaly (1926), Bensley and Vimtrup (1928) and Krogh and Vimtrup (1932). In the 1920's therefore, it was practically an established fact that the Rouget cells accounted for independent capillary activity. The first step toward refuting this belief occurred when Florey and Charleton (1926) and Barksdale (1926) demonstrated through the differential staining experiments that it was doubtful if the Rouget cells accounted in any degree whatsoever for capillary contractility.

Later workers began to doubt, furthermore, the power of capillaries to contract independently. Clark and Clark (1932), Sandison (1932) and Clark and Clark (1935), (1940)

observing vessels in the transparent chambers in the rabbit's ear, could find no evidence of active contractility in any of the capillaries that were observed. Fulton and Lutz (1940) working on the retrolingual membrane of the frog proved that there was no endothelial contraction, even after nerve stimulation or direct electrical and mechanical stimulation. They pointed out that the capillary blood flow is regulated in a sphincter-like manner with periodic opening and closing of the junctions, without the aid of the supplying vessels. This sphincter, a muscular structure, is similar in function to the Rouget cells as described by Bensley and Vimtrup (1928).

Gradually workers have been reversing their opinions. Among them are Chambers and Zweifach (1944) who describe a mechanism for controlling the rate and amount of blood flow through the capillaries.

The main function of capillaries is as a medium of exchange between nutrient materials and body wastes. In certain organs, however, there is a predominance of specialization. (Chambers and Zweifach, 1946). These deviations are great enough so as to obscure the nutritive pattern.

Table I (Chambers and Zweifach, 1946) gives a description of the more generalized type of capillary bed, attempting to present it as an organized unit. This would indicate that the true capillaries with their deviations or specialization in the various organs are side-branches of the

predominantly nutritive type of capillary bed which makes up the central channel.

The purpose of this paper is to present the varying degrees of specialization of capillary patterns in selected regions within the body.

Fig. 1. Capillary from the mesentery of a frog. (Redrawn after Ranvier, from Maximow and Bloom, 1944.)

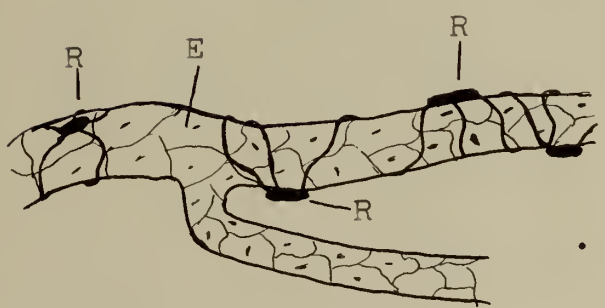


Fig. 2. R: Rouget cell.
E: Capillary endothelial wall.
(Redrawn after Krogh.)

TABLE I (See Fig. 3)

VASCULAR COMPONENTS OF THE TERMINAL CIRCULATION IN THE RAT MESOAPPENDIX (Chambers and Zweifach, 1946)

(Dimensions given are of diameters)

I. Terminal Arteriole (ca.20-25 microns)

Coat: muscular, single, continous layer.

Movements: pulsations related to larger arteries, but less regular.

II. Capillary Bed

1. Metarteriole (ca. 8-15 microns) (initiating thoroughfare a-v channel).

Coat: muscle cells, typical, discontinuous.

Movements: Vasomotion, with slow, constrictor-dilator phases.

Branches: Precapillary junctions (ca. 5-12 microns) twisted, outflowing.

Coat: muscle cells, typical, acting as sphincters.

Movements: Vasomotion, independent of metarterioles.

Lead into True Capillaries.

Coat: endothelial

Movements: passive and tonic

2. Proximal Segment of a-v Channel.

Coat: muscle cells, atypical.

Movements: No vasomotion, responsive only to abnormal stimuli.

Branches: a. Precapillary Junctions.

Coat: muscle cells, atypical.

TABLE I (Continued)

Movement: similar to a-v.

Lead into true Capillaries.

b. Capillary Junctions, outflowing, same structure as and continuing as True Capillaries.

3. Distal Segment of a-v Channel.

Coat: connective tissue.

Movements: passive, slight.

Branches: Postcapillary Junctions, inflowing, same structure as and originating from True Capillaries.

4. Non-muscular Venules (ca.15-25 microns) (fusion of thoroughfare channels).

Coat: Pronounced connective tissue.

Movements: passive, slight.

III. Muscular Venules (ca. 25-30 microns)

Coat: muscle cells and connective tissue.

Movements: Highly responsive, varicose contractions.

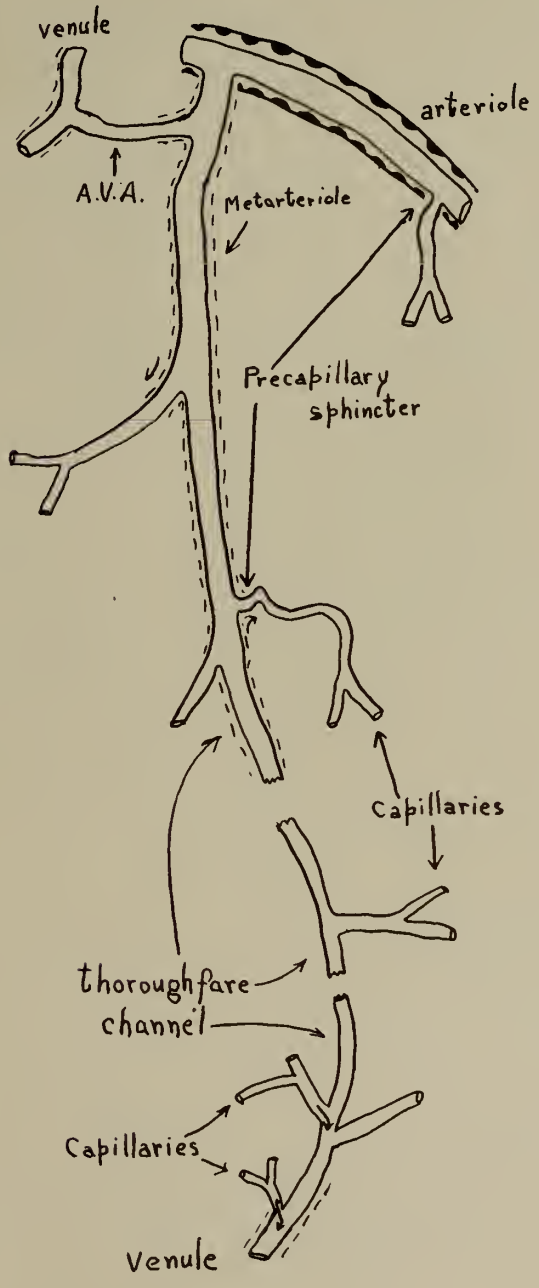


Fig. 3 (in conjunction with TABLE I). Diagram of a functional unit of the capillary bed, together with a metarteriolar-venular anastomosis (A-V-A) and a precapillary branching off directly from an arteriole. (After Chambers and Zweifach, 1944).

CAPILLARY PATTERNS IN THE KIDNEY GLOMERULI

In part one, mention was made of the fact that by definition, a capillary is a purely endothelial tubing, normally found between an arteriole and a venule.

In the structure of the kidney however, we find a capsule into which an afferent arteriole enters, branches and rebranches. Here, the blood vessel loses its muscular coating and becomes purely endothelial in structure. This endothelium is partly syncytial (Vimtrup, 1928). Each capillary loop is covered by a basement membrane on which rest the visceral epithelial cells. The blood vessel in the glomerulus is semi-permeable, and has all the characteristics of a true capillary. When the vessel leaves the capsule, it again has the morphology of an arteriole. It becomes a true capillary only when it encircles the tubule, (Fig. 4), breaking up into a network of capillaries. It then becomes a venule as it continues to the interlobular vein.

The wall of the afferent arteriole has specialized smooth muscle cells forming a cuff before the capillaries branch. These smooth muscle cells, 25-85 microns in size, are called juxtaglomerular cells. (Winton and Bayliss, 1935). These are absent in the lower vertebrates and in children under two years of age.

The pattern within Bowman's Capsule is as follows:

According to Stricker (1872), the vas afferens enters the capsule and divides into four to eight branches which widely diverge as they run toward the neck. Each branch divides, and these secondary branches come together gradually toward the center to form the vas efferens. It was believed, (Stricker, 1872) that after the vessel enters the capsule and divides, the branches anastomose. Sappey (1879), however, upon the examination of sixty-five kidneys, found no anastomosis.

Opinion changed, however. Ebner (1902) believed that anastomosis was present. Johnston (1902) in his drawing of a reconstruction of the glomerulus of a kidney showed numerous anastomoses. Disse (1902) agrees with Johnston and Ebner, and Roost (1912) published a reconstruction from the glomerulus of a dog, showing the presence of anastomosis.

The author, in figures 5 and 6, has shown what he believes to be the probable patterns formed by anastomosing and non-anastomosing glomerular blood vessels, if it were possible to remove and spread them out.

Vimtrup (1928), in his examination of over one million glomeruli never once found evidence of anastomosis. (Fig. 7). He pointed out that under low power focussing the branches of the vessels appeared to anastomose. He stated: "As the vessels are curled and twisted around one another they may be so interwoven that the high power binocular microscope is necessary in order to observe with certainty that they are

in reality separate." (Fig. 8).

The glomerular vessels are extremely specialized in permeability when compared to the usual capillary wall (Winton 1937). This would account for their highly efficient filtration activity.

TABLE II

TOTAL NUMBER OF GLOMERULI AS FOUND IN CERTAIN MAMMALS
(after Vimtrup, 1928)

Cat	202,813
Albino rat	33,826
Dog	407,155
Human child (1 yr.)	887,339
Adult Negro	833,992
Adult White: I	867,177
Adult White: II	1,233,320

TABLE III

SIZE OF GLOMERULI AS FOUND IN CERTAIN MAMMALS
(after Vimtrup, 1928)

Man	159-300 microns
Cat	102-124 microns
Rabbit	34-191 microns
White Rat	124-127 microns

According to Vimtrup, the shape of the glomeruli is more or less globoid. In man and rabbit, it is ovoid or flattened. In dog, it is usually oval.

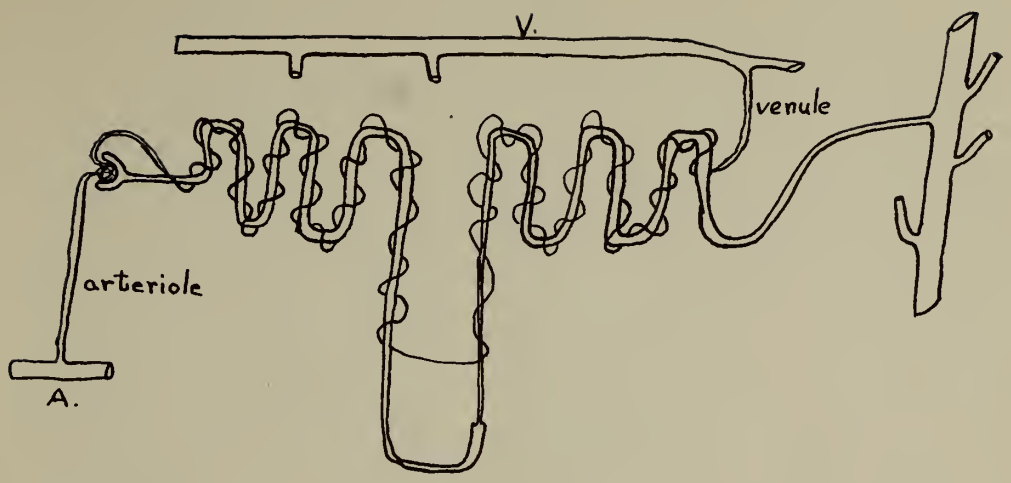
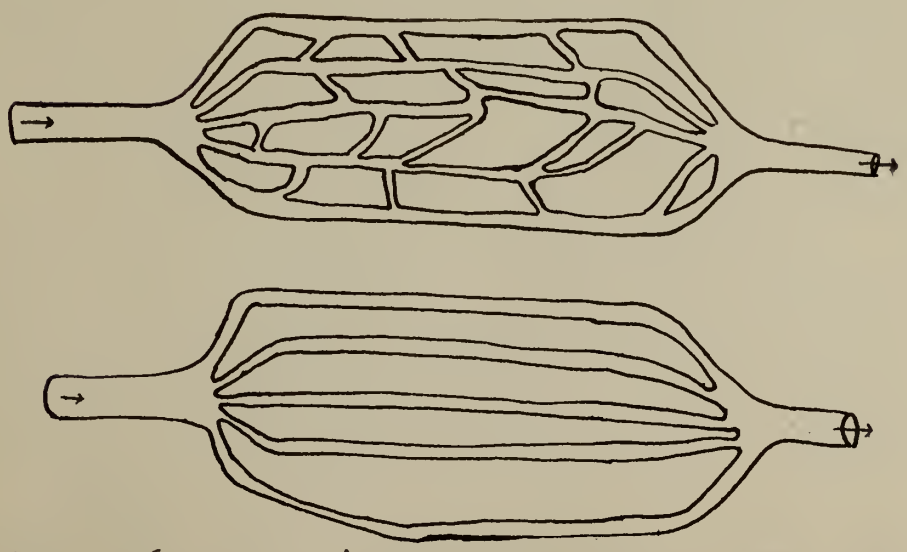


Fig. 4. Diagrammatic drawing of the capillary blood supply to the tubules of the kidney glomerulus. (Redrawn and modified from Winton and Bayliss.)



Figs. 5-6. Author's version of the probable patterns formed by anastomosing and non-anastomosing blood vessels in the kidney glomerulus. Direction of blood flow is also shown.

Under certain pathological conditions, the blood supply furnished the tubular tissue is independent of the glomeruli (MacNider, 1927). According to Vimtrup (1928), the only blood reaching the tubules in mammals is from the glomeruli. In amphibians, however, the renal-portal veins which arise from veins in the legs pass to the kidneys and form a capillary network around the tubules. (Singer, 1933).

In aglomerular kidneys, a capillary network which arises from branches of the dorsal aorta forms the "glomus". These vessels then collect into venules, eventually fuse and return to the heart by way of the postcardinal vein. (Edwards, 1928).

Marshall (1934) believes that obliteration of the glomerular vessels results in atrophy of the tubules. It was found by Winton (1937) that administration of a diuretic or an anti-diuretic respectively increased or decreased the number of glomeruli functioning up to one hundred per cent. It is not entirely impossible that further research in this field may lead to important discoveries regarding kidney pathology.

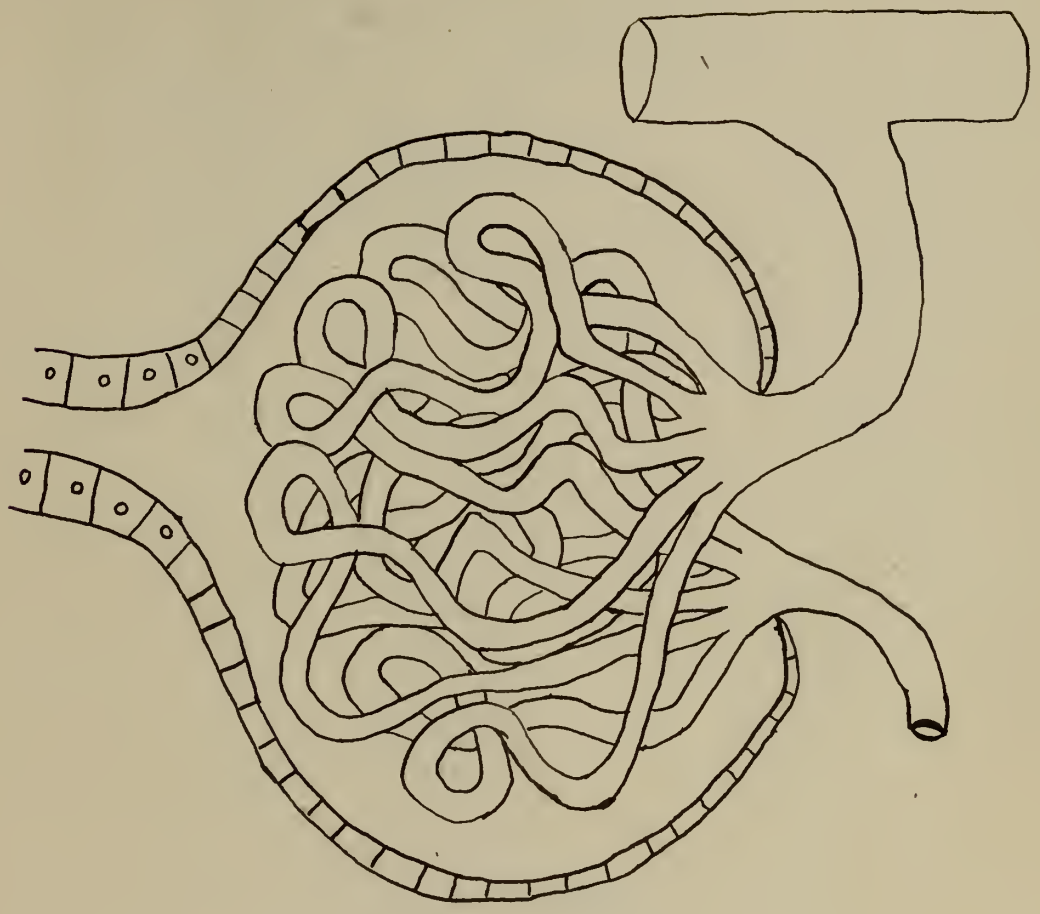


Fig. 7. Diagram of the arrangement of the capillary loops in a glomerulus, showing how the loops are twisted, and the absence of anastomosis. (From Vimtrup: "Glomeruli In Kidneys Of Man And Mammals".)

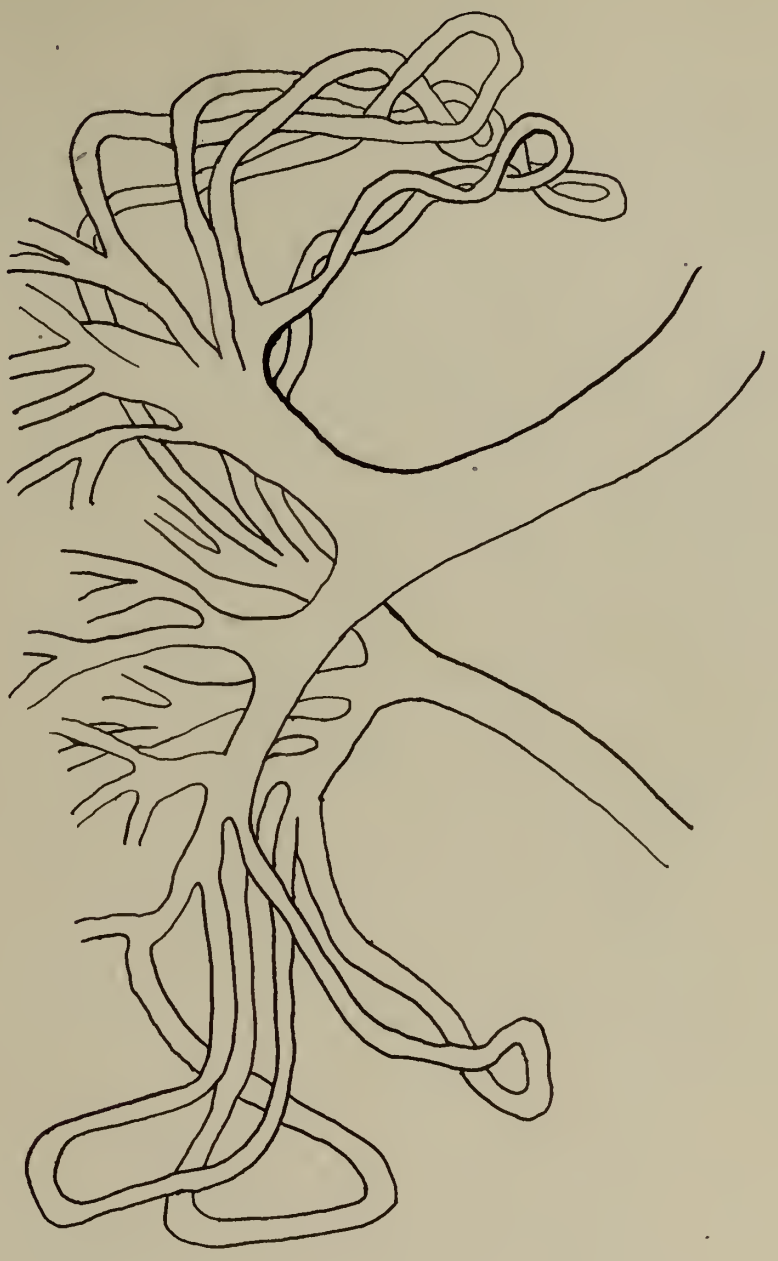


Fig. 8. Semidiagrammatic representation of the mode of branching of the vas afferens and the vas efferens of a glomerulus. (After Vimtrup:"Glomeruli In Kidneys Of Man And Mammals".)

CAPILLARY PATTERNS IN THE INTESTINAL VILLI

In the kidney glomeruli, the function of the blood vessels is filtration. The capillaries in the villi of the intentine, however, serve an entirely different purpose. The surfaces of the villi are specialized primarily for absorption. (Mall, 1888).

According to Noer (1943), the study of circulation in the small intestine has received very little attention. Textbooks differ somewhat in their descriptions, but the general plan is as follows:

> According to the fifth edition of Cunningham's "Textbook of Anatomy", (1930), "Each villus is covered by a layer of columnar cells, set upon a basement membrane, and under this is a fine layer of longitudinal non-striated muscle, continuous with the lamina muscularis mucosae of the intestine.
>
> "In the interior of each villus is a central sinus, a space lined with endothelium, continuous with the lymphatic vessels (chyle vessels) of the mucosa. There may be several such lymph spaces within the larger villi.
>
> "A network of blood-vessels lies between the epithelium and the central sinus.
>
> "Dilation of these vessels causes enlargement of the villus, while contraction of the muscular layer diminishes its height and serves to assist in emptying the central

sinus into the lymphatic or chyle channels."

The blood supply is as follows: An arteriole enters each villus. From this a capillary plexus arises from which the blood is returned by one or two larger venules (Maximow and Bloom, 1944). There is no twisting or looping of the capillary vessels as was found in the kidney. There is, however, free anastomosis. (Fig. 9 and Fig. 10).

The villi are outgrowths of the mucus membrane. In man, they have a length of 0.5 to 1.5 millimeters. They are barely visible to the naked eye, and according to Mall (1888), may vary from 10-40 per square millimeter.

Their shape varies according to their location. According to Maximow and Bloom (1944), in the duodenum the villi are wide, leaflike structures arranged with their long diameter in the transverse direction and in alternating longitudinal rows. (Fig. 9). In the ileum, they gradually acquire a finger-like form. (Fig. 10). Many villi are divided at the top into two or more lobes by slits which extend for varying distances into the villi. This way, the villi can increase in number during the growth of the intestine.

This would mean, therefore, that the capillary patterns in the villi differ according to their specific location, and to the age of the individual.

Differing from the blood vessels in the glomeruli of the kidneys, the capillaries in the intestinal villi are not

the only vessels entering into the physiological process of absorption carried on by the villi. This is also done by the lacteals leading from central lymphatic vessels into which nutriment from the digestive tract is absorbed. (Carey, 1920 and 1921). Amino-acids and glucose are absorbed into the capillaries; about sixty per cent of the digested fat passes into the lacteals. (Barclay, 1934).

Numerous lymphocytes have been found between the epithelial cells in the villi. (Baron and Chambers, 1935; Field and Drinker, 1936; and Florey, Wright and Jennings, 1941). Since the lymphocytes may give rise to macrophages, (Jordan and Burrows, 1946), it is possible that an added function of the capillary vessels in the villi is to aid the intestinal secretions in combatting many types of pathogenic bacteria.

Fig. 9. Blood supply to and from the villi in the duodenum of man. (Redrawn and modified after Schaffer.)

Fig. 10. Blood supply to and from the intestinal villus in the ileum. (Redrawn and modified after Mall.)

— Venule

— Arteriole

— Capillary

CAPILLARY PATTERNS IN THE SKIN

In the skin, the capillaries form an entirely different pattern than in either the kidney glomeruli or the intestinal villi. The capillary loops which are formed in the dermal layer of the integument are not dependent upon one particular arteriole for their supply. Rather, there is free branching of the several arterioles from the arteries which are located in the subcutaneous layer. (Fig. 12).

According to Maximow and Bloom (1944), branches of these arteries reach upward, form a network (rete cutaneum) on the boundary line between the derma and the hypodermis; this is parallel to the surface. From one side of this network, the vessels enter at the boundary between the papillary and reticular layers where they form the thicker subpapillary network. (Fig. 11). This, in turn, gives off thin branches which enter the papillae and form networks inside them.

Where hair is present, each hair sac has its individual blood vessels. (Hoepke, 1927). The hair sacs are supplied with blood from three sources: The first is from a small artery giving off a capillary network into the papilla. (Figs. 13, 14). The papilla consists of cellular connective tissue. The network formed here by the capillaries, is quite dense, allowing a full supply of blood to reach the follicle. (Danforth, 1939). The second source of supply of blood to the hair is from the rete subpapillare facing the hair sac. The

other source of supply is from a number of small arterioles which form a dense capillary network in the connective tissue layer of the follicle.

According to Cowdry (1928), the origin of the dermal layer of the skin which is that portion of the integument containing the greatest proliferation of capillary vessels, is mostly from the peripheral portion of the somites, which is from the mesenchyme.

There are no blood vessels to be found in the epidermal layer. (Figs. 11 and 12). The epidermis receives its nutrition from the fluid part of the blood which circulates between the cells of the stratum granulosum. (Hoepke, 1927). (Fig. 11).

According to Krogh (1921), the blood supply of the skin is under the control of a nervous mechanism which can either dilate the arterioles, thus increasing the supply of blood to the skin, or diminish the amount of blood by constricting the small arteries. When the supply of blood to the skin is increased, a greater number of capillary vessels are functioning. If the quantity of blood is diminished, the lumina of a great number of capillaries are closed. Thus, the capillary patterns formed are much more complex when the arterioles are dilated, than when they have contracted. (Krogh, 1921), (Cowdry, 1928), (Edwards and Duntly, 1939).

Lewis (1924), however, found that the capillary pattern in the skin changes very little from time to time.

He believes that even if the blood flow is decreased the vessels are still pervious. Lewis reasons that the blood flow through the skin is supplemented through a greater dilation of vessels that had previously been present, than by the opening of capillaries that had been closed.

There are many factors influencing the nervous control over the integumental arterioles; thus causing temporary physiological changes in the capillary pattern. Among these factors are emotional state of the individual, poisons (including alcohol), improper diet, and diseases. (Krogh, 1921).

Many chemicals also influence cutaneous vascular reactions. Lewis (1924) in his many experiments has demonstrated the effect of histamine on the blood vessels of the skin. This produced the responses which were characteristic of mechanical injury. Dale (1929) suggests that acetylcholine from within the body may have some effect by its dilatory effects on blood vessels.

According to Lewis (1924), the capillary loops do not ordinarily determine the complexion of the skin. The venous plexus presents a greater area which is parallel to the surface, even though lying deeper. The capillary loops are usually at right angles to the skin surface.

A major function involving the capillary vessels in the skin is their influence on the temperature of the skin. According to Best and Taylor (1936): "The radiation of the body's heat is carried out principally through the medium of

the cutaneous vessels."

All the above factors would be involved in influencing temporary physiological changes in the capillary patterns in the skin.

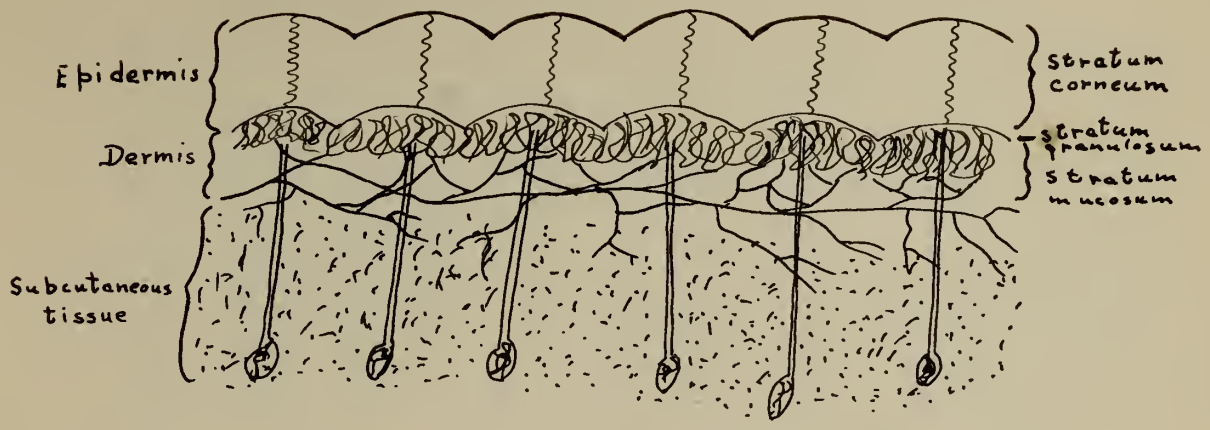


Fig. 11. Microscopic section of the skin. (From Edwards and Duntley, after Berres.)

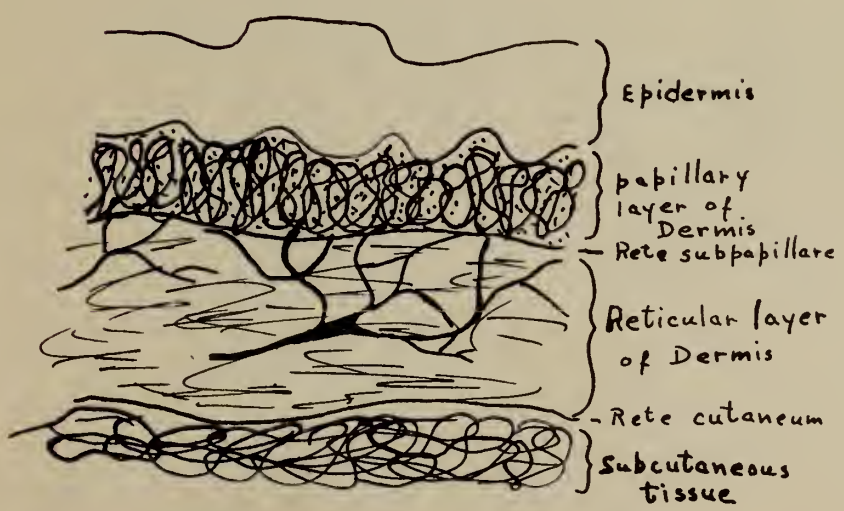


Fig. 12. Distribution of the blood vessels in the skin. (Modified after v. Brunn.)

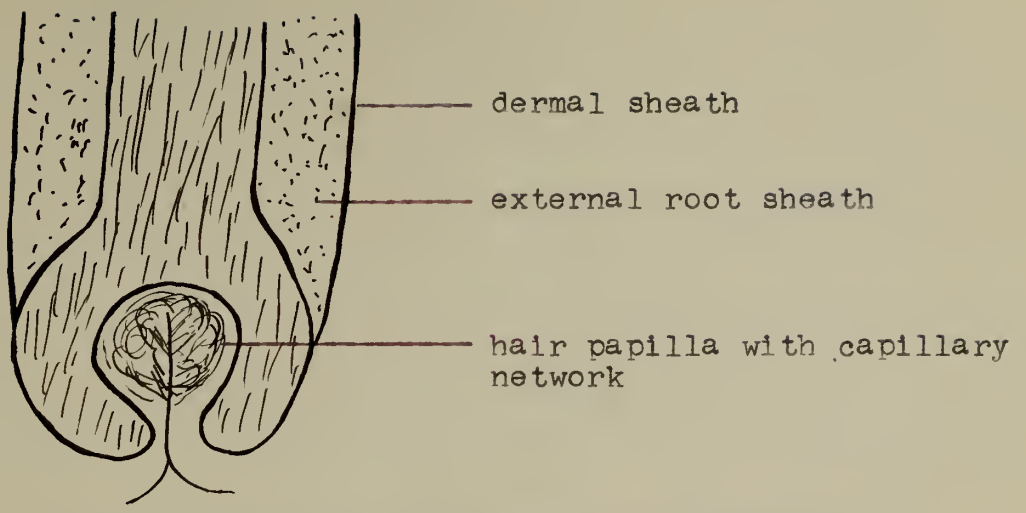


Fig. 13. Root of hair (long. sec.) showing capillary network in the hair papilla. (After Schaffer.)

Fig. 14. Diagrammatic closeup of hair papilla showing capillary pattern. (Modified after Schaffer.)

CAPILLARY PATTERNS IN SKELETAL MUSCLE

Blood vessels supplying skeletal muscle tissues are enormous in number. According to Tiegs (1934), the capillary vessels directly surround the individual muscle fibers and form a dense network with meshes that stretch along the entire length of the fiber. In many instances, the arrangement of the capillary vessels may cause them to run perpendicular to the muscle fibers. (Fig. 15).

Striated muscular tissue in mammals arises from the mesoderm and especially from its primitive segments. (Maximow and Bloom, 1944). Cells known as myoblasts give rise to the muscle tissue. It is not yet known definitely in what manner the skeletal muscle fibers arise from these cells. Capillary vessels arise from the connective tissue fascia surrounding the fiber bundles. (Tiegs, 1934).

Krogh (1919), did a considerable amount of work on muscle capillary morphology. He found, for example, that when India ink was injected into the capillary vessels and certain parts of the tissue stimulated, while other portions were excised after the excitation, the increase in the number of open vessels in the excised tissue was very great. He showed that in a resting muscle, a relatively small number of capillaries can be seen. (Fig. 16). In instances where red blood cells were present, but the walls of the enclosing

vessels had constricted, the cells were pressed into an elongated form. (Fig. 16).

When the muscle was stimulated, Krogh demonstrated the fact that many vessels which had previously been invisible now came into view. Thus, he believed that the blood flow through the tissues would be increased several fold, assuring an adequate oxygen supply for the contraction process. He believed, therefore, that the shape and size of the capillary vessels differs greatly, depending upon the physiological condition of the muscle.

Lewis (1924), however, as it was previously pointed out, believes that definite conclusions cannot be drawn regarding changes in capillary patterns, since he has demonstrated in the skin that all the vessels are pervious, whether the blood flow is small or large.

It may be possible, however, that the specialized morphology of capillaries in the skin is different from that in the muscles. It would thus account for the fact that the specialized function of muscle capillaries is quite different from that of the skin capillary vessels.

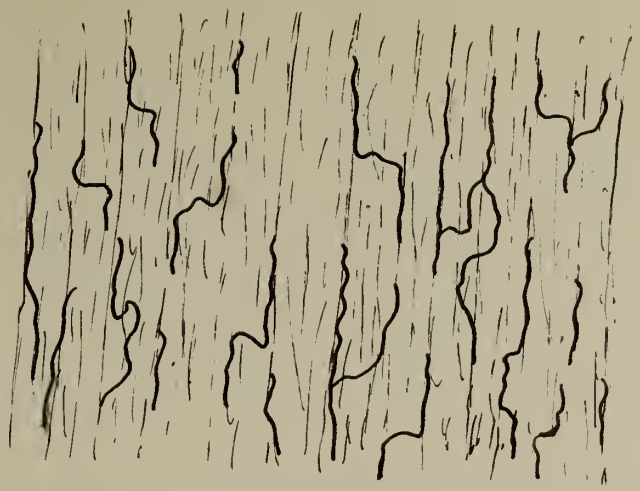


Fig. 15. Blood vessels in striated muscle, showing arrangement of vessels parallel to muscle fibers and right angle branching. (Slightly modified after Maximow and Bloom.)

Fig. 16. Muscle capillaries of guinea-pig vitally injected with India ink. Walls of capillaries not shown. Blank oval areas represent red cells most of which are distorted in shape. (After Krogh.)

CAPILLARY PATTERNS IN THE INTESTINAL MESENTERY

The intestinal mesentery is almost a plane surface. For this reason, it is an excellent region in which to study capillaries and the circulation of the blood in general. Since the tissue consists of a thin membrane, its capillary network is arranged in the same plane. (Landis, 1933). According to Zweifach and Kosmann (1937) and Chambers and Zweifach (1944), there is considerable branching and anastomosis of the capillary vessels. These two investigators did considerable work on the topography of the rat mesentery. They found that in a region where capillaries are discernible, occasionally vessels of capillary dimensions were observed where the blood was flowing more rapidly than through the capillaries adjacent to them. These, they believed, were varicose venules where along their proximal portions they exhibited relatively slow and variable changes in diameter. It is thought that many investigators have mistaken these venules for independently contracting capillaries. A detailed examination of the intestinal mesentery capillary blood flow is presented in Figure 1 and in Table 1.

Figure 17 is from the author's own observations while working on the intestinal mesentery of the frog. According to Chambers and Zweifach (1944), the capillary pattern in the mammalian mesentery is quite similar to that in

the frog; the only exception being that the capillary vessels in the mammal are smaller, corresponding with the smaller diameter of the red blood cells..

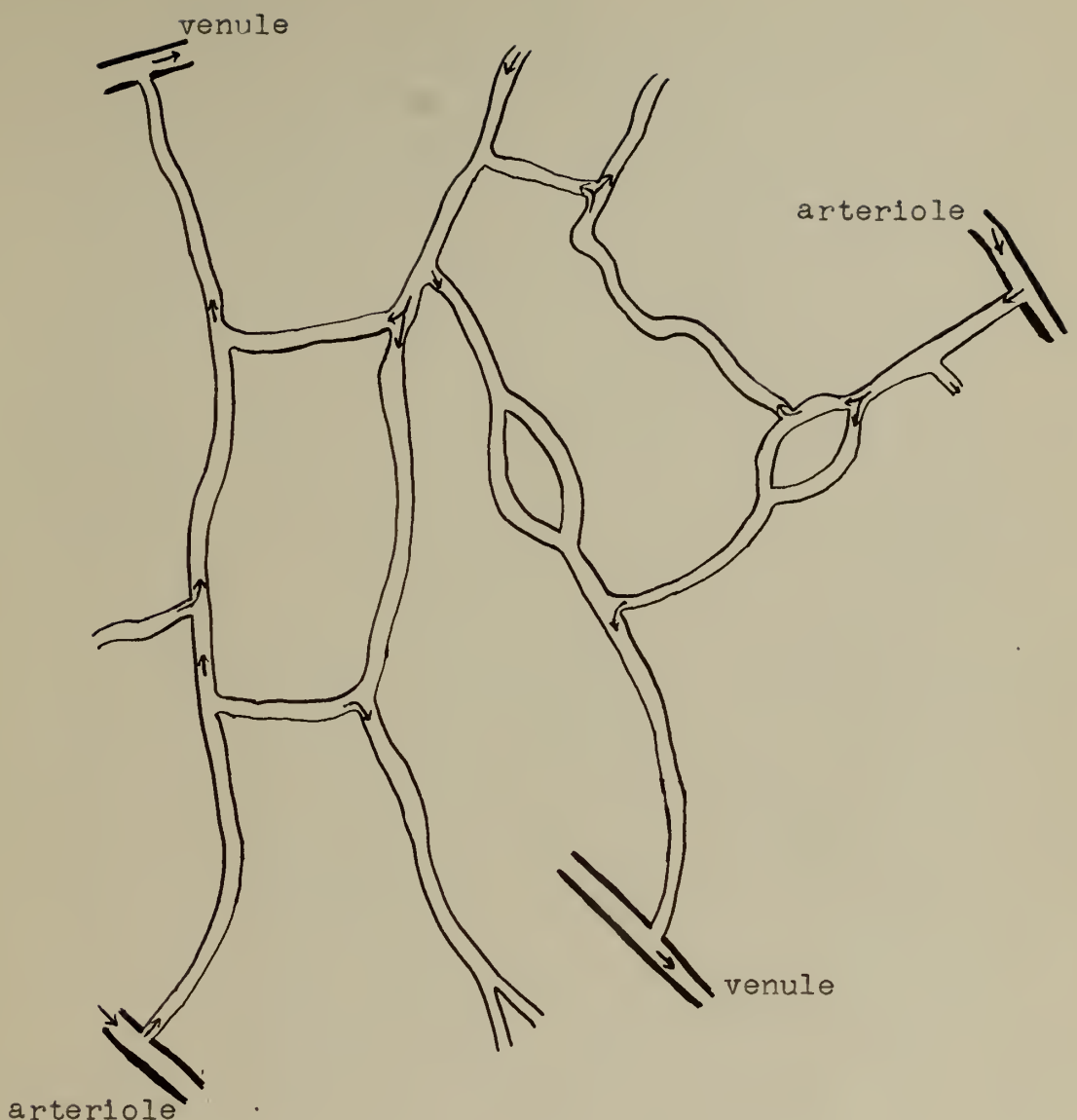


Fig. 17. Capillary pattern in the intestinal mesentery of the frog, showing branching and anastomosis and direction of blood flow. (Drawn from the author's own observations.)

RESEARCH DONE BY THE AUTHOR

THE MEASUREMENT OF THE SURFACE AREA OF CAPILLARIES IN THE INTESTINAL MESENTERY OF THE FROG

According to Krogh (1929) "----the arrangement of capillaries is so complicated that the difficulties in the way of even approximate measurement are very formidable."

With the above statement in mind, the author shall present the procedure that he used, as was suggested to him by his adviser, Dr. B. R. Lutz. The work consisted of measuring the capillaries while the frog was anesthesized. Circulation could be observed while the actual measurements were being made.

The first step was to calibrate the microscope. This was done as follows: A graduated micrometer eyepiece was placed in the 10X ocular of the microscope. Using a 26X water-immersion objective, focussing was centered upon a micrometer millimeter slide. It was found that 68.3 divisions on the graduated eyepiece in the ocular were equal to one-half millimeter on the micrometer millimeter slide. Since one-half of a millimeter is equal to 500 micra, that meant that one division on the graduated eyepiece would be equal to 7.32 micra.

The next step was to devise a formula to use in measuring the actual surface area of the capillaries. Knowing

that diameter times pi equals circumference, length times circumference equals surface area.

PREPARATION OF THE FROGS

The frogs were injected with .6-.8 cc. urethane (20%), depending upon the size of the frog. The frog was then placed in a paraffin filled glass dish containing a transparent circular block to use as a window. Lateral incisions, approximately 5 mm. long were made in the right abdominal walls of skin and muscle, and the intestine was carefully drawn out. The small intestine was then pinned around the edge of the circular block, so that the mesentery around the intestine was spread out over the block. Extreme caution had to be used to avoid stretching the mesentery in any way. This whole area was then flooded with frog Ringer's solution, and placed under the water-immersion objective of the microscope. The objective was carefully lowered into the solution and focussed. Observations were then begun.

All the capillaries within a circular area of 68.3 divisions or 500 micra were measured. The size of the area was found as follows: Since 500 micra equal the diameter, 250 micra equal the radius. The area of a circle is equal to pi times the radius squared. The area in which the capillaries were measured each time, therefore, was 196,000 square micra or .196 square millimeters. It was also made a point to measure adjoining areas so that results

could be obtained within a large area.

RESULTS

The results proved to be much higher than were anticipated. In the ten frogs worked on, the average capillary surface area was found to be 44.6% of each .196 square millimeters of mesentery.

The calibration of the microscope and the results of the first measurements were checked by Dr. Lutz. It may be possible that the injection of urethane may have had some effect on the size of the capillaries, since urethane is a vasodilator. Although the capillaries themselves do not contract or dilate actively, their size may have been affected by the dilation of the neighboring arterioles. Atypical result may also have been caused by irritation through mechanical stimulation.

The author's adviser suggested the frogs be single-pithed. This was done on one frog, and the circulation within the mesentery stopped completely. There was no evidence of circulation even in the larger vessels; the venules and arterioles. A number of capillaries in this frog were measured, nevertheless, and the result was 45.6% capillary surface area; approximately the same as in the anesthetized frogs.

Below are given the individual results that were obtained from each of the ten frogs in which a number of capillaries in the intestinal mesentery were measured:

1. 47% of the surface area that was measured.
2. 40% of the surface area that was measured.
3. 50% of the surface area that was measured.
4. 49% of the surface area that was measured.
5. 52% of the surface area that was measured.
6. 38% of the surface area that was measured.
7. 38% of the surface area that was measured.
8. 44% of the surface area that was measured.
9. 43% of the surface area that was measured.
10. 45% of the surface area that was measured.

This gives an average of 44.6% of the total area that was measured.

CAPILLARY PATTERNS IN OTHER ORGANS

SPLEEN

The distribution of blood vessels within the spleen is as follows: According to Krumbhaar (1926), after the main splenic artery and splenic vein enter at the hilum, each vessel divides into branches. These are supported by the branching trabeculae. (Fig. 18). As these divide, each supports a branch of an artery and an accompanying vein. Small branches from these arterioles enter the red pulp. These then divide into short vessels, the "penicilli". The terminal portion of each penicillus is an endothelial tube which unites with the sinusoids. These have a wide irregular lumen which contracts to the smaller and uniform caliber of the common capillary. Moreover, the capillary endothelial cells become associated with the flat reticular cells lining the sinusoids.

Some investigators believe that there is an open arrangement of blood vessels in the spleen. (Thiel and Downey, 1931; Krumbhaar, 1926). They believe that the blood passes freely into diffuse lymphoid tissue of the red pulp. The sinusoids join complete venous capillaries which continue into smaller venules projecting through the red pulp and enter the trabeculae. Others support a closed system, believing that the sinusoidal wall is extremely permeable, allowing

relatively free movement of the various cells. (Barcroft, 1925).

LIVER

According to Johnson (1918), the hepatic cells pour their secretions into a network of small canaliculi, running between adjacent faces of cells forming the cords. The afferent vessels entering at the hilum divide into large interlobular branches. These vessels then give off smaller interlobular branches which follow the septa between the lobules. The inter-lobular branches of the portal veins give off short branches passing to the surface of the lobules where they break up into an intralobular network. (Fig. 19). This network is made up of hepatic sinusoids with wide lumina. They anastomose irregularly separating the cords from one another. Thus, each cell may have two or more sinusoids in contact with it: These carry the blood to the center of each lobule. They then empty it into the central vein emerging at the base of the lobule. Lining the walls of the sinusoids are endothelial cells and Kupffer cells. The latter are believed to be part of the reticulo-endothelial system. (Kupffer, 1899). Rouget cells are also believed to be from this same system. Future investigators may well inquire into the possibility of some connection between Kupffer cells and Rouget cells.

LUNGS

The capillary arrangement in the lungs is extremely specialized. Briefly, however, the pattern is as follows: According to Wearn, Ernstene, Bromer, Barr, German and Zschiesche (1934) and Maximow and Bloom (1944), most of the blood to the lungs is provided through the pulmonary arteries. Branches of these accompany the bronchi and their branches to the respiratory bronchioles. Here, they divide and a branch passes to each alveolar duct and is distributed in a capillary network over all the alveoli communicating with this duct. (Fig. 20). The venules arising from the capillaries of the pleura and those of the alveolar septa and portions of the alveolar ducts and running into the interstitial connective tissue fuse to form the pulmonary veins. In the alveoli arising from the bronchioles the capillaries anastomose between the terminations of both the pulmonary and bronchial arteries.

CEREBRUM

According to Scharrer (1944), the vertebrate brain may be vascularized either by single arteries and veins which anastomose into a capillary network, or by paired blood vessels ending in capillary loops. In mammals, the vascularization is by single arteries and veins anastomosing into a capillary network.

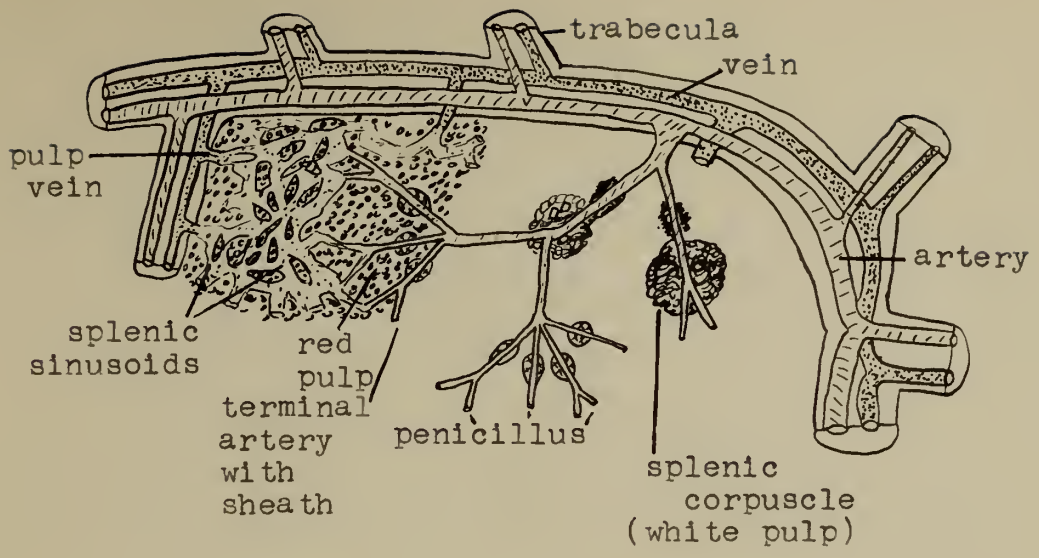


Fig. 18. Diagram showing pattern of circulation in the spleen. (Redrawn from Kendall.)

Fig. 19. Diagram of cross-section of liver lobule, showing convergence of capillaries toward central intralobular vein (IL). (Redrawn and modified after Kendall.)

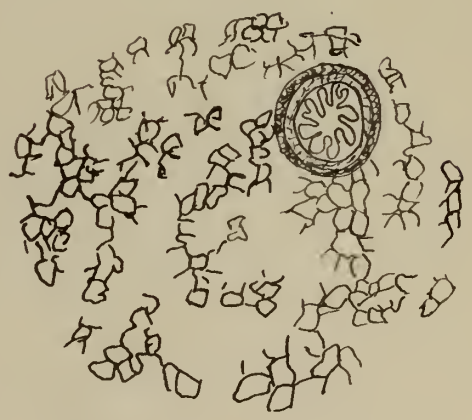


Fig. 20. Drawing from a slide made by the author showing the capillary network in the lung of Hamster.

SUMMARY

The history of the study of blood vessels is traced back to Harvey and Malpighi in the seventeenth century. Following the discovery of capillaries, study of these minute vessels was neglected until a much later date. New theories relating to the study of capillaries are constantly being evolved. One of these theories is the belief that capillaries are specialized morphologically for diverse functions within the body.

The shape of the endothelial cells making up the capillary wall differ according to the location of the vessel and its particular function. Pericapillary cells known as Rouget cells have, at times, been observed. The belief that these cells are responsible for active contractility of the capillaries has long been under dispute. Most recent workers find no evidence that capillaries show any active contractility.

In the mammalian kidney, the afferent arterioles which enter the glomeruli and branch and rebranch take on capillary characteristics then leave as efferent arterioles. There are two theories regarding anastomosis of the branching arterioles in the glomeruli. Investigators formerly believed that anastomosis occurred when the arteriole branched within the glomerulus. Recent workers, however, give ample evidence for lack of anastomosis.

The glomeruli differ greatly according to the classes

within vertebrates. Even in mammals, the number, size and shape of the glomeruli differ according to the order. Through continued research in the field of glomerular filtration, important discoveries are possible regarding kidney pathology.

In the villi of the intestines, the capillaries are supplied by a central arteriole. There is no twisting or looping of the capillary vessels as is found in the kidney glomeruli. There is, however, free anastomosis. The shape of the villi and consequently the pattern of the capillaries within the villi will vary depending upon the location of the villi in the small intestine.

In the skin, the portion of the integument containing the greatest number of blood vessels originates in the mesenchyme. Each hair sac in the skin is supplied with its own individual blood vessels. Temporary physiological changes in the capillary pattern in the skin can be brought about as a result of several extrinsic factors.

The capillary vessels in the skeletal muscle form dense networks. A great number of capillaries that had seemed to be previously closed, appear to open when the muscle tissue containing these vessels is stimulated.

The capillary blood flow through the intestinal mesentery is relatively simple to study due to the fact that this tissue has a plane surface. Here, there is free branching and anastomosis of the capillary vessels. At times, varicose

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venules which may be mistaken for capillaries may be observed within the mesentery. With a few possible exceptions, the capillary pattern in the mammalian mesentery is similar to that in the frog.

In his research work, the author found that the average capillary surface area per unit area of the frog mesentery was forty-four per cent of the surface area that was measured. This is a good deal greater than what may normally be expected, but several extrinsic factors may have been involved.

In the spleen the "penicilli" unite with the sinusoids. These have wide irregular lumina. There are two diverging opinions concerning the arrangement of blood vessels in the spleen. One holds for an open circulation, the other for a closed system.

In the liver, the interlobular networks continue dividing until they form an intralobular network which consists of hepatic sinusoids.

In the lungs, there is considerable specialization of the capillary vessel system. Branches from the pulmonary arteries accompany branches of the bronchi to the respiratory bronchioles. At the respiratory bronchioles, the arterioles divide and are distributed over the alveoli in a capillary network. The alveolar capillaries anastomose between the terminations of the pulmonary and bronchiole arteries.

The blood supply to the mammalian cerebrum is by means of single arterioles. These branch and anastomose into several capillary networks. Blood leaves the cerebrum through single venules.

ABSTRACT

The paper deals with the capillary patterns that are formed within certain organs in the vertebrate body.

In the introduction a brief history is given commencing with Harvey's discoveries in the seventeenth century. In recent investigations, new theories have beenevolved, one of the most recent being that capillaries are specialized morphologically in different parts of the body.

The Rouget cell theory, long under dispute, seems destined for oblivion, since recent investigators have found no evidence of active capillary contractility.

The most recent work in relation to the mammalian kidney holds to the belief that there is no anastomosis of the branches of the blood vessel after it enters the glomerulus. There is a vast difference in glomerular morphology among the several classes of vertebrates.

The capillaries in the intestinal villi are supplied by a central arteriole. The capillary patterns in the intestinal villi differ according to the specific location of the villi in the intestine.

In the skin, there is considerable looping of the capillary vessels. Each hair sac is supplied with its own individual blood vessels.

The capillaries in the skeletal muscle form dense

networks with much branching and anastomosis.

The capillaries in the intestinal mesentery are on a plane surface, and consequently, are relatively simple to study. Here, there is free branching and anastomosis of the capillary vessels.

In the author's research work, it was found that the average capillary surface per unit area of the frog mesentery was forty-four per cent of the total surface area that was measured.

In the spleen, there are penicilli uniting with the sinusoids. It is debatable whether the system of circulation in the spleen is open or closed.

The interlobular networks in the liver divide until they form an intralobular network.

In the lungs, the pulmonary arterioles branch and are distributed over the alveoli in a capillary network. These capillaries, in turn, branch and anastomose.

The mammalian cerebrum is supplied by single arterioles which branch and anastomose into several capillary networks.

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